THE ECOLOGICAL IMPORTANCE OF THE RHEOTACTIC REACTION OF STREAM ISOPODS.

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CONTENTS.

EARLIER WORK ON RHEOTAXIS IN ISOPODS.

Some time ago it was shown that the stream mores of the isopod *Asellus communis* (Say) is usually positive in its rheotactic reaction ('12).[1] When measured in an intermittent circular current[2] this was shown by the relatively high percentage of positive responses (79 per cent. of 1,570 trials). In a continuous straight current the same tendency was shown by the relatively long time (7 hrs., 12 min.) which stream isopods would remain positive before their ultimate reversal. Pond isopods of the same species, on the other hand, gave weak positive reaction in the intermittent current (25 per cent. of 775 trials) and there was an average of only 51 minutes of positive reaction before reversal in a continuous straight current.

The difference in the reaction of the isopods from the two habitats is closely correlated with certain natural conditions, the most important of which is the oxygen content of the water. The oxygen tension of the streams which isopods inhabit is much higher than that of the ponds. Laboratory tests show that increasing the amount of oxygen present in water makes pond isopods more positive and decreasing the oxygen tension tends to make stream isopods less positively rheotactic.

But even under uniform and favorable external conditions

[1] Numerals standing alone have reference to earlier papers by the author.

[2] For details of the method see Allee, '12, p. 276; '13, p. 261.

not all stream isopods are positive all the time and some individuals show more daily variations than others ('13*a*). These variations have been analyzed by means of the resistance of isopods to potassium cyanide ('14) and by the rate of carbon dioxide production accompanying different degrees of positive rheotactic reactions (Allee and Tashiro, '14). These analyses indicate clearly that the degree of positiveness of the rheotactic reaction of an isopod is closely correlated with its rate of metabolic activity; that a highly positive rheotactic reaction is correlated with a relatively rapid rate of metabolic activity and that when either internal or external conditions interfere with the metabolic rate of the isopod, the rheotactic reaction becomes less positive.

There are certain periods in the life cycle of stream isopods when the positiveness of the rheotactic reaction is markedly reduced. These may or may not be due to the metabolic conditions obtaining at the time. The young isopod either disregards or is very erratic in its response to a water current until it is about a month old ('12). Later at the frequently recurring molting periods the same tendency is shown for about five hours preceding and following the molt ('13, '13*a*). The breeding period is also a period of weakened positive rheotactic response ('12) in which the stream isopods lose about two-thirds of their positiveness.

The breeding season begins rather later in the stream than in the pond mores ('11) but it is in full swing in April and early May. By late May the adults become rare but the season's young may be taken one third or more grown. These young isopods are at first indefinite in their rheotactic reactions. They become highly positive more rapidly in water which has a high oxygen tension but they will come to be highly positively rheotactic even if confined to pools that have a low oxygen content ('12).

Survey of Stream Distribution of *Asellus communis* in the Chicago Area.

I have studied the local distribution of *Asellus communis* in the Chicago area only (Shelford, '11, '13, maps). Most of the stream isopods used in the experimental studies summarized

above were taken from the County Line Creek, which flows into Lake Michigan near Glencoe, Illinois. About three sixteenths of a mile above its mouth the creek branches and its total length, including tributaries, is about half a mile. This is a physiographically young stream in the intermittent rapids, permanent pool stage with numerous stones scattered over its bed. It is ranked by Shelford ('13) as the third in age of his series of twenty-six stations in the study of stream ecology.

Stream isopods also occur in the following streams:

1. Pettibone Creek, a large stream north of the County Line Creek. Shelford ranks this as next older than the County Line Creek in his physiographic series. In many ways it resembles the younger stream but is more permanent and contains less sewage. The isopods are much less abundant.

2. North Branch of the Chicago River at Des Plaines, Illinois. Shelford ranks this as a "moderately swift medium-sized stream" and as station 16 in his stream series of 26 stations. When visited in August, 1911, the stream was reduced to a series of pools without connection, hence the part visited was younger than Thorn Creek. The isopods were found among the numerous stones on the bottom of the pools.

3. Thorn Creek at Thornton, Illinois. Shelford lists this as station 12 in his stream series. This is a rapid permanent stream about 20 feet wide at ordinary flow. There is much sewage present from Chicago Heights. The isopods here are scarce, being confined to (*a*) protruding roots under overhanging banks; (*b*) under the edge of rocks in the wide shallow riffles; (*c*) in embayments or among relatively permanent catches of drift. This stream represents about the largest, oldest stream in which the stream mores of these isopods can maintain themselves. Isopods may occur in very old streams of the sluggish base-level type, as in the Fox River at Cary, Illinois, but the part of the stream in which they are found is ecologically equivalent to a mature pond (Station 35, p. 34; Shelford '13).

From this study of the streams which contain isopods it was found that the stream mores of *Asellus communis* are most numerous in young streams of the intermittent rapids, permanent pool type; especially those that contain some sewage, and that

they become more rare as the streams become larger until they are entirely lacking in many streams of the Thorn Creek stage of development. Also they are not found in streams that do not afford a good chance for lodgment.

The distribution of isopods shows a decided seasonal variation in the County Line Creek which is the only one of the streams listed above which has been sufficiently studied to give conclusive evidence on this point. In the dryer periods they are of course limited to the pools. When the stream is flowing they tend to scatter over the bottom among the debris or under overhanging banks where they may congregate in large numbers clinging to protruding roots. During the summer period the isopods are often collected in large groups along the edge of the masses of leaves that have been gathered and forced together by the spring floods. During late summer and early autumn they may be easily collected by finding and securing these groups. Later in the autumn the isopods tend to occupy the whole stream, crawling over the bottom and among the new fallen leaves. In the spring they are still more widely scattered.

Relation of Rheotaxis to Maintenance of Position in Streams.

How much of this seasonal and regional distribution is determined by the rheotactic reaction *per se?*

In 1908 the entire County Line Creek was dry except the pool nearest the lake. The rainfall of the following spring was normal. Shelford ('11) found that under these conditions the fish had all been driven to the lowest pool and in 1909 only one species, the horned dace (*Semotilus atromaculatus*) had made any progress upstream and that only about three rods. In July, 1909, the isopod *A. communis*, was found in the second permanent pool from the source and was abundant a quarter of a mile from the lake.

The horned dace is much more efficient in its rheotactic reaction than is *Asellus*, hence this distribution further towards the headwaters of a stream that was dry the preceding year must must be accounted for by some other factor than rheotaxis. Stream isopods if placed on a dirt bottom in a pan of water that

is allowed to dry, will burrow into the moist mud and thus escape death for some time and it is highly probable that they were able to survive the drouth of 1908 in this manner and to take up their usual places though in less than their usual numbers with the late autumn rains.

Another line of evidence that tends to minimize the importance of rheotactic reaction in the ecology of stream isopods is found in the analysis of the reaction itself. In 6,630 discontinuous minute reaction periods 95 per cent. of which resulted in positive rheotactic responses the average rate of movement was 76 cm. per minute. The current in which these trials were made averaged 472.5 cm. per minute, hence this represents the response to a mild current. When exposed to the continuous action of a straight current of about this strength the most positive stream isopods reversed their reaction and became negative in less than twenty-four hours. As the rate of the current was increased in laboratory tests the isopods came to rest and clung to the bottom, making no effort to advance. This reaction was given before the current became as strong as that found in parts of the County Line Creek.

These observations show that positive rheotaxis may enable isopods to maintain their position for a time in parts of a stream having a weak current but after continued exposure or in strong currents the clinging reaction becomes the more important one. This is in accord with the fact that isopods are only found in streams having abundant places for support (p. 55). If the clinging reaction is essential for the most positively rheotactic adults, it must be much more so for the early juvenile stages and for adults in the breeding season or during the molting period when the positive rheotactic reaction is either weakened or entirely absent.

There is no correlation between the seasonal variation in the positiveness of the rheotactic reaction and the seasonal distribution, as described for the County Line Creek, but the distribution can be fully accounted for by the seasonal variation in places of lodgment and surfaces that give a good foothold for crawling, that is to say in the seasonal changes in the distribution of leaves in the stream. Thus in seasonal as in regional dis-

tribution thigmotaxis seems to be of primary importance rather than rheotaxis.

Interrelations of Thigmotaxis and Rheotaxis.

In testing for interrelations between the rheotactic and thigmotactic reactions of isopods that might prove of ecological importance the following methods were employed: Isopods were tested individually in an intermittent circular current for their rheotactic reaction; immediately following this the individuals were tested in a straight trough to find how strong a water current they could resist.

These tests were made in a wooden trough painted with water proof paint over which fine quartz sand had been sprinkled while the paint was soft in order to give a good surface for the isopods. The sides met at the bottom forming a V-shaped trough with an enclosed angle of about thirty degrees. The trough was 75 cm. long and was used with a pitch of 8 cm. The current was produced by tap water.

In making the test the isopod was oriented as desired in a very small stream of water. A rubber tube 5 mm. in diameter connected with the tap faucet was introduced 5 cm. above the isopod. The faucet valve was gradually opened until the current swept the isopod off its feet. This occurred in less than a minute so that fatigue did not affect the result. Then the flow in cubic centimeters was measured. In the early work five successive tests were averaged to give the resistance of the isopod for the day but this was found to be too severe and in the later work only one test was made per day.

In the weak current the isopods would usually start to move in the direction in which they were headed ('12) although those oriented negatively attempted to turn more often than the others. They usually continued moving until the current became fairly strong, then stopped and clung to the boards in the angle at the bottom of the trough.

When headed upstream the head was placed close to the bottom as movement ceased the head and front of the thorax made an arch which kept the water running over the relatively smooth convex back of the isopod. The anterior legs are used more in

clinging than the posterior ones, which act as braces. When thus clamped the isopods withstood a flow as high as 6,600 c.c. per minute under the conditions of the experiment. Sometimes they failed to clamp when headed positively but this occurred less often than in any other position. The speed of the current successfully resisted appeared to fully equal or surpass the most rapid flow at usual stream levels in those streams in which the isopods are abundant.

When oriented negatively the isopods may clamp and withstand a strong current (up to 3,959 c.c. per minute as compared with 6,600 c.c. per minute when oriented positively). In this reaction the abdomen is bent downward much as is the head when the animal is turned in the opposite direction, but it is more easily forced up than the head and hence this is a less efficient method for clinging. Isopods fail to clamp more often under these conditions than when headed positively. This may be due to the difference in length of the posterior and anterior legs. The latter are short and can take more active part in the clamping reaction than can the longer posterior ones. The failure to clamp allows the negatively oriented isopods to be more often swept off their feet by a relatively slow current.

Comparative tests of the average clinging efficiency of isopods oriented positively and negatively support the evidence given by the maximum clinging ability under the two conditions. The results of these tests which were made under identical conditions are given in Table I. The orientation of the isopod was alternated to equalize a possible fatigue effect. In every case except isopod No. 170 the strength of the current resisted when the isopods were headed upstream was approximately double that necessary to sweep the negatively headed isopods off their feet. An average of 64 tests on 10 different isopods shows that a flow of 2,534 (± 72) c.c. per minute was required to sweep a positively oriented isopod off its feet while 1,385 (± 92.6) caused those headed negatively to lose their footing. In other words a positively oriented isopod is approximately twice as efficient in maintaining its position in a stream as is one oriented negatively.

There are indications that isopods could maintain themselves

TABLE I.

Showing the effect of orientation upon the strength of current in which isopods can maintain their position. These tests were made under entirely identical conditions throughout. In testing each animal, one to three trials were made with the isopod facing in one direction then the orientation was reversed and an equal number of trials were made. This was done to equalize possible fatigue effects. For further details of the method used see p. 57.

Oriented Positively.

Trials.	Identification No.									
	168	169	170	171[1]	172	21	22	23	168	173
1	4,750	1,300	2,750	2,750	4,350	3,000	2,100	1,140	4,033	3,450
2	3,350	2,400	2,000	2,500	2,850	2,160	1,800	1,500	2,200	2,100
3	4,000	3,400	1,800	2,000	3,850	1,500	2,100	1,620	2,550	3,450
4		1,500	3,750	2,700	3,300	2,280	2,280	2,580	2,490	3,300
5		2,400	2,350	2,500	3,300	1,560	5,100	2,820	3,530	3,900
6						540	1,800	3,000	3,240	
7							2,000	2,280		
8							2,160	1,950		
9							1,800	1,800		
10							2,160	1,560		
11							2,280	2,400		
12							900	1,920		
Average .	4,033	2,200	2,550	2,490	3,530	1,973	2,207	2,072	3,007	3,240

General average of 64 trials, 2,534 ($\pm$ 72)

Oriented Negatively.

Trials.	Identification No.									
	168	169	170	171[1]	172	21	22	23	168	173
1	3,300	600	3,050	850	200	1,500	2,160	1,440	1,800	200
2	1,900	600	2,500	450	300	2,040	600	1,380	1,360	200
3	200	1,400	3,950	1,900	350	1,860	360	300	2,610	200
4		2,500	1,800	1,050	2,700	1,080	420	1,200	850	2,800
5		1,700	2,650	2,750	3,600	2,280	1,920	1,260	1,430	2,800
6						1,920	2,760	360	1,240	
7							300	1,080		
8							1,920	600		
9							600	1,800		
10							300	2,520		
11							300	1,760		
12							200	600		
Average .	1,800	1,360	2,610	850	1,430	1,780	987	1,192	1,547	1,240

General average of 64 trials, 1385 ($\pm$ 82).

in quite strong currents when headed at right angles to them. In doing this an isopod used the feet of one side as anchors and swung below them. This method of maintenance gave erratic results with the apparatus used. It also brought the isopod

[1] Copulating pair.

into different relations with the current since when oriented transversely part of the body would be near the surface instead of the whole body being at the bottom, as is the case when the animals are oriented either positively or negatively. Since with the present apparatus it was impossible to obtain comparable results and since stream isopods usually go either positive or negative this method of maintenance will not be discussed further.

The data so far presented make it evident that the rheotactic reaction *per se* is not sufficient to account for the maintenance of position of stream isopods but that it has an effect upon the clinging ability of isopods in the current that is very important. In other words the movement accomplished in the rheotactic reaction of isopods is of much less importance in maintaining their position in streams than is the sign of the rheotactic reaction, which becomes of prime importance by means of its influence upon the clinging ability of isopods. Since the sign of the rheotactic reaction is closely correlated with the metabolic rate of isopods it follows that an isopod with a relatively high rate of metabolism would give positive rheotactic responses and hence be better able to maintain its position in a stream than an isopod having a relatively low rate of metabolism which would be accompanied by negative or indefinite rheotactic reactions.

It has already been noted that there are two periods in the natural life of adult stream isopods when the usual highly positive rheotactic reaction is lowered, namely: the breeding season and the shorter but more frequently recurring molting period. Both of these times are the more critical in that the clinging ability is, or may be, directly affected by them. During and immediately after molting an isopod is easily swept off its feet by a water current and in the breeding season at the time of copulation the pairs have their clinging ability reduced, especially when oriented negatively (cf. No. 171, in Table I., p. 59). After the female liberates the young and before the brood pouch is molted, a bubble of air may get into it and an isopod thus afflicted finds it almost impossible to remain on the bottom even in quiet water. These floaters often occur in the laboratory and have been observed to some extent in nature. Thus both the molting period and the breeding season reduce the maintenance efficiency

of stream isopods, directly by decreasing the clinging ability and indirectly by decreasing tendency to orient positively in the current which in turn affects the clinging ability of the isopod.

The rheotactic reaction has been shown to vary with the changing metabolic state of the isopod (Allee and Tashiro, '14). The clinging power of positively oriented isopods also varies to a limited extent, with the degree of positiveness of the rheotactic reaction. This is shown by the data exhibited in Tables II. and III. In Table II, the average rheotactic response

TABLE II.

Showing the relation between low and high clinging ability of positively oriented isopods and the rheotactic reaction. For details of methods see pp. 57 and 61.

Responses Compared.	No. Trials.	Ave. Current Resisted.	Average Rheotactic Reaction.				Ave. Efficiency.[3]
			+	—	a	o	
Current resisted 3,500 c.c. per minute or more...........	65	4,418	78 (±2.6)	18	4	0	2.7
Current resisted, 2,000 c.c. per minute or less............	99	1,497	57 (±2.6)	23	10	10	2.3

of isopods that resisted a current of 3,500 c.c. per minute or more is compared with that given by isopods that were swept off their feet by a current of 2,000 c.c. per minute or less. The isopods with the higher clinging power averaged 78 per cent. positive in their rheotactic reactions and they did not fail to give the rheotactic response when stimulated. On the other hand the isopods with the poorer clinging power averaged 57 per cent.

[3] In order to have a method for measuring and recording the efficiency of movement of isopods in the current during rheotactic tests the following arbitrary standard was adopted, which represents numerically the distance covered in a minute's reaction period. The following values were applied to the numbers:

0, no reaction.
1, slight movement.
2, any response between 1 and 3.
3, progress one third around the pan positively (approximately 27 cm.) or two thirds, negative (54 cm.).
4, progress two thirds around the pan positive, or one and one third negative.
5, progress once around the pan positive, or twice around negative.
6, any distance over 5.

Experiments showed that isopods oriented negatively covered twice the distance per leg movement as did those oriented positively.

positive and gave no response to the current in 10 per cent. of the trials. Thus the rheotactic reaction averaged 21 per cent. less positive when the isopods had the lower clinging power. Since this is four times the probable error it must be accepted as strongly indicating that isopods with high clinging ability when positively oriented, tend to give a higher percentage of positive rheotactic reactions than those with low clinging power.

The converse data of this relationship is shown in Table III,. which lists the average current strength necessary to sweep isopods off their feet that had given: (*a*) highly positive rheotactic reactions; (*b*) low positive rheotactic reactions; (*c*) a high percentage of failures to respond to the current. In all cases the only variation known was in the metabolic state of the isopods.

TABLE III.

Showing the relation between clinging ability of positively oriented isopods accompanying a rheotactic reaction of 60 per cent. or more positive; 40 per cent. or less positive: and 40 per cent. or more no reaction. For details of method see pp. 57 and 62.

Responses Compared.	No. Trials.	Ave. Rheotactic Reaction.				Ave. Efficiency.[4]	Ave. Current Resisted.
		+	—	*a*	o		
Rheotaxis 60 per cent. or more positive	160	90	6	4	0	2.7	2,898 (±66)
Rheotaxis 40 per cent. or less positive	87	13	45	22	20	2.1	2,230 (±81)
Rheotaxis 40 per cent. or more no reaction	21	5	1	15	79	0.24	1,990 (±109.5)

The data presented in Table III., show that isopods having a 13 per cent. positive rheotactic reaction gave 23 per cent. less clinging ability than those that were 90 per cent. positive in their rheotactic reactions. With isopcds that gave a high degree of inaction in the rheotactic tests there was a further reduction in the clinging power. The change in the strength of current successfully resisted is not at all proportional to the variation in the rheotactic reaction with which it is compared but the difference in clinging power accompanying high and low positiveness of the rheotactic reaction is 4.5 times the probable error and is therefore significant.

[4] For explanation of average efficiency see footnote 3, p. 61.

Not enough data has been collected to warrant any conclusions being drawn regarding the possible relationship between the clinging ability of isopods and their metabolic rate as measured either by their resistance to potassium cyanide or their carbon dioxide production. However the data given in Tables II. and III. show that there is a variation in the clinging power of positively oriented isopods accompanying more or less closely the variation in the positiveness of the rheotactic reaction. Since the degree of positiveness of this reaction depends on the rate of metabolism (*loc. cit.*) it seems fair to conclude that there is some correlation between the physiological states of isopods and their ability to maintain themselves in a water current. This means that a decrease in the metabolic activities of isopods not only causes a decrease in the positiveness of the rheotactic reactions and hence indirectly decreases the clinging power of isopods in a current (p. 60) but that it also directly decreases the clinging power.

Discussion.

In all probability the sum total of the reactions of an organism largely determines its distribution (Shelford and Allee, '13; Wells, '14). With different animals in different environments now one reaction or group of reactions may be the more important and now another. It is obvious that the maintenance of position is of primary importance in the distribution of stream animals and it is likewise obvious that this must be done either by some means of clinging or by the rheotactic reaction or by a combination of the two. Bryozoa show the maximum development of the clinging reaction while certain fishes as *Notropis* show a maximum development of the rheotactic response since they rarely rest on the bottom (Shelford and Allee, '13). A study of maintenance methods of stream animals would probably establish a completely graded series between these two extremes. In such a graded series all crawling animals, to which group the isopods belong, would of necessity depend a great deal upon their ability of clinging to the substratum to maintain themselves.

To what extent positive orientation in the rheotactic response increases the clinging efficiency of crawling stream animals other than isopods is a matter for experimentation. Judging solely from

structure it would seem entirely probable that such long bodied animals as *Hydropsyche* larvæ, dragon-fly or may fly nymphs and stone-fly nymphs would show this correlation to some extent. Among fishes, the bottom resting darting fishes of the type represented by *Boleosoma* and *Etheostoma* should also show this correlation. Further experimentation on these forms would probably demonstrate, as the experiments here reported for isopods, that the sign of the rheotactic reaction continues to be of prime importance in the problem of maintenance of position in streams long after the rheotactic movements have ceased to be significant.

How much of this behavior of stream isopods is an adaptation to life in streams? In order to get the problem clearly stated perhaps a recapitulation of relationships is permissible. By means of their highly positive rheotactic reactions the stream isopods are better enabled to maintain themselves in the stream environment through the interaction of the rheotactic and thigmotactic reactions. This tendency to give positive rheotactic reactions is much weaker in pond isopods and can be modified within certain bounds in both pond and stream mores by varying the oxygen tension of the water. Therefore it seems that this is not a specific adaptation for stream habitation which the isopods exhibit, but rather that adaptation (perhaps better called property), of all living matter namely, irritability (Mathews, '13). Beyond that, the isopod is no more adapted to the stream environment by reason of its positive rheotaxis than the stream is adapted to the isopod by virtue of presenting the complex of environmental conditions (high oxygen and low carbon dioxide tension) best calculated to call forth and maintain positive rheotaxis. Environmental conditions automatically cause an isopod to give those responses which fit it to maintain its position in the stream.

Summary.

1. The distribution of the isopod *Asellus communis* cannot be accounted for by its rheotactic reaction alone, but can be accounted for by the interacting thigmotactic and rheotactic reactions.

2. The movements given in rheotactic reactions of isopods are

of secondary importance in their maintenance of position in streams.

3. The sign of the rheotactic reaction is of primary importance in this regard in that an isopod oriented positively can withstand approximately twice the current strength of one oriented in the opposite direction.

4. The clinging ability of positively oriented isopods varies somewhat with the degree of positiveness of the rheotactic reaction which in turn is closely correlated with the metabolic conditions of the isopods.

5. The molting period and breeding season are especially important in the ecology of stream isopods in that they directly decrease the clinging ability and indirectly affect it by lowering the tendency to give positive rheotactic reactions.

6. Beyond possessing irritable protoplasm isopods are no more adapted to the stream environment by reason of their positive rheotaxis than the stream is adapted to the isopod by virtue of presenting the complex of environmental conditions best calculated to call forth and maintain positive rheotaxis.

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